EFFECTS OF SALINITY ON ESTABLISHMENT OF *POPULUS FREMONTII* (COTTONWOOD) AND *TAMARIX RAMOSISSIMA* (SALTCEDAR) IN SOUTHWESTERN UNITED STATES

Patrick B. Shafroth[1], Jonathan M. Friedman[1], and Lee S. Ischinger[1]

ABSTRACT.—The exotic shrub *Tamarix ramosissima* (saltcedar) has replaced the native *Populus fremontii* (cottonwood) along many streams in southwestern United States. We used a controlled outdoor experiment to examine the influence of river salinity on germination and first-year survival of *P. fremontii* var. *wislizenii* (Rio Grande cottonwood) and *T. ramosissima* on freshly deposited alluvial bars. We grew both species from seed in planters of sand subjected to a declining water table and solutions containing 0, 1, 3, and 5 times the concentrations of major ions in the Rio Grande at San Marcial, NM (1.2, 10.0, 25.7, and 37.4 meq l⁻¹; 0.11, 0.97, 2.37, and 3.45 dS m⁻¹). Germination of *P. fremontii* declined by 35% with increasing salinity ($P = .008$). Germination of *T. ramosissima* was not affected. There were no significant effects of salinity on mortality or above- and belowground growth of either species. In laboratory tests the same salinities had no effect on *P. fremontii* germination. *P. fremontii* germination is more sensitive to salinity outdoors than in covered petri dishes, probably because water scarcity resulting from evaporation intensifies the low soil water potentials associated with high salinity. River salinity appears to play only a minor role in determining relative numbers of *P. fremontii* and *T. ramosissima* seedlings on freshly deposited sandbars. However, over many years salt becomes concentrated on floodplains as a result of evaporation and salt extrusion from saltcedar leaves. *T. ramosissima* is known to be more tolerant of the resulting extreme salinities than *P. fremontii*. Therefore, increases in river salinities could indirectly contribute to decline of *P. fremontii* forests by exacerbating salt accumulation on floodplains.

Key words: exotic species, Tamarix ramosissima, Populus fremontii, *river salinity, seedling establishment, Rio Grande, riparian vegetation, Bosque del Apache National Wildlife Refuge.*

In the last century the exotic shrub saltcedar (*Tamarix ramosissima* Ledebour) has spread throughout southwestern United States, where it now dominates many riparian ecosystems (Bowser 1958, Robinson 1965). In many areas *T. ramosissima* has replaced stands dominated by the native Fremont cottonwood (*Populus fremontii* Wats.; Campbell and Dick-Peddie 1964, Ohmart et al. 1977), decreasing the habitat of Neotropical migrant birds (Anderson et al. 1977, Cohan et al. 1978) and altering fluvial processes (Graf 1978, Blackburn et al. 1982). Understanding the factors controlling establishment of *T. ramosissima* and *P. fremontii* can aid in managing these species.

Successful invasion by *Tamarix* in the Southwest has been attributed to many factors. Much of the early spread probably resulted from the coincidental timing of clearing of *P. fremontii* stands by early settlers and the availability of *Tamarix* seed (Campbell and Dick-Peddie 1964, Harris 1966, Horton and Campbell 1974, Ohmart et al. 1977). Subsequent spread resulted largely from effects of damming and channelizing southwestern watercourses. Reductions in the magnitude of high flows and associated reductions in channel movements decreased the formation of bare, moist alluvial bars, which provide ideal *P. fremontii* seedling habitat (Ohmart et al. 1977, Stromberg et al. 1991). Smaller peak flows have also reduced leaching of salts from floodplain soils (Busch and Smith in press), perhaps favoring the salt-tolerant *Tamarix* (Everitt 1980, Brotherson and Winkel 1986, Jackson et al. 1990). Flow regulations that have altered the historical timing of peak flows may have inhibited *P. fremontii* regeneration because of its short period of seed dispersal and viability in early summer (Horton 1977, Everitt 1980), but they have enhanced *Tamarix* regeneration because of its abundant seed production throughout the growing season (Merkel and Hopkins 1957, Tomanek and Ziegler 1962, Warren and Turner 1975, Horton 1977). Finally, successful invasion of *T. ramosissima* has been attributed to its superior ability to resprout following fire (Busch and Smith 1993).

We conducted experiments to examine the influence of river salinity on germination, survival, and growth of *Populus fremontii* var. *wislizenii* (Rio Grande cottonwood) and *T. ramosissima* on freshly deposited alluvial bars, the principal habitat for seedling establishment of both species. Field observations have suggested that *P. fremontii* is more negatively affected by high salt concentrations than *T. ramosissima* (Brotherson and Winkel 1986, Anderson 1989). Laboratory studies have confirmed this difference by exposing seedlings and cuttings of these species to varying concentrations of NaCl and $CaCl_2$ (Jackson et al. 1990, Siegel and Brock 1990). Two factors potentially confound the relationship of results of laboratory studies to field conditions. First, the mix of salts found in riparian ecosystems typically includes many constituents other than Na, Ca, and Cl. In many plants, salinity effects result from toxicity of specific ions as opposed to osmotic stress (Greenway and Munns 1980). Second, moisture availability is lower and more variable in the field than in these laboratory studies. This factor is important because low soil water potential caused by high salinity is exacerbated by low soil moisture content. We addressed these concerns by exposing *T. ramosissima* and *P. fremontii* seedlings to four different concentrations of a mix of salts designed to mimic ion concentrations in the Rio Grande. The experiment was conducted outdoors in planters subjected to a controlled water-table drawdown. Experimental conditions were designed to simulate alluvial bars along the Rio Grande in central New Mexico, where once-extensive *P. fremontii* forests have largely been replaced by *T. ramosissima* thickets (Campbell and Dick-Peddie 1964). Our outdoor experiments were supplemented by studies of germination under similar salinity treatments in the laboratory.

METHODS

Seedling establishment experiments were conducted outdoors in 1993 near Fort Collins, CO, at latitude 40°35′ north, longitude 105°5′ west, and elevation 1524 m. Twelve 122 × 92-cm (diameter × depth) epoxy-lined steel tanks contained six 30 × 100-cm planters made of PVC pipe. Holes 1.26 cm in diameter were drilled into the lower 10 cm of each planter to allow water exchange, and the planters were filled to 92 cm with washed coarse sand (approximately 6% gravel [>2000 μm], 78% sand [$>300–2000$ μm], 16% fine sand [$>75–300$ μm], and <1% silt and clay).

Four salinity treatments were each replicated in three tanks (12 tanks total). Each tank contained three planters of *P. fremontii* var. *wislizenii* and three of *T. ramosissima*. Thus, the experimental unit for each species was a group of three planters within a tank. To avoid pseudoreplication, responses were measured as the mean value of the three planters. The results for the two species were analyzed as separate, completely randomized experiments with four treatments and three replicates per treatment.

The tanks were filled with water from the Cache la Poudre River (a snowmelt stream low in dissolved solids), and solutions containing multiples (0, 1, 3, and 5 times) of the mean concentration of all major ions in the middle Rio Grande were made. These four solutions constitute treatments 0x, 1x, 3x, and 5x. Mean ion concentrations were derived from eight measurements from the conveyance channel at San Marcial, NM, between October 1989 and September 1991 (U.S. Geological Survey 1991, 1992). The following salts were added to make treatment 1x: 309.9 mg l^{-1} $CaSO_4*2H_2O$; 302.4 mg l^{-1} $NaHCO_3$; 122.0 mg l^{-1} $MgCl_2*6H_2O$; 70.1 mg l^{-1} NaCl; 13.9 mg l^{-1} K_2SO_4. Because the coarse sand substrate was low in nutrients (cf. Segelquist et al. 1993), 15 mg l^{-1} of Fisons Technigro fertilizer (16% N, 17% P, 17% K) was added to every tank.

At the time of planting and for 1 wk thereafter, the water level was 10 cm below the soil surface. A 3.5-cm-week^{-1} drawdown rate was applied for the remainder of the growing season (17 June to late September). Water-table drawdowns are associated with summer declines in discharge along western streams. The 3.5-cm-week^{-1} drawdown rate was selected because a previous study (Segelquist et al. 1993) indicated that it is within the optimal range for establishment and growth of plains cottonwood (*Populus deltoides* ssp. *monilifera*).

Flowering panicles of *T. ramosissima* were collected on 17 May at the Bosque del Apache National Wildlife Refuge (latitude 33°46′ north, longitude 106°54′ west, elevation 1375 m). The panicles were air-dried for 48 h to enhance opening of seed capsules. Collected material was sifted through a series of soil

screens until clean samples of seeds were obtained. Catkins of *P. fremontii* were collected at the Bosque del Apache on 1 June. The catkins were air-dried for 72 h to enhance opening of seed capsules. Capsules were placed between soil screens and seeds were separated from the cotton and capsules using forced air. Seeds of both species were sealed in plastic containers and refrigerated at 5°C (Zasada and Densmore 1977). On 10 June, 100 *P. fremontii* seeds were planted in each of three planters per tank, and 200 *T. ramosissima* seeds were planted in each of the other three planters.

Electrical conductivity (EC) and temperature were measured using a Yellow Springs Instrument Co., Inc., Model 33 S-C-T meter, and pH was measured using a Corning 105 hand-held pH meter in conjunction with a Corning ATC temperature probe and a Corning general purpose combination electrode. EC was measured weekly in every tank begining 12 June (17 measuring dates). Whenever EC was measured, a representative water temperature for that day was determined by averaging the temperature values from five randomly selected tanks. All EC measurements were corrected for temperature and reported at 25°C. Fourteen weekly measurements of pH were made beginning 30 June. On 16 June, 14 July, 18 August, and 17 September, water samples from one randomly selected tank per treatment were analyzed to determine concentrations of Ca, Mg, Na, K, CO_3, HCO_3, Cl, SO_4, and NO_3. Ca, Mg, Na, and K were determined by inductively coupled plasma emission spectroscopy (ICP; EPA method 200.0, United States Environmental Protection Agency 1983); CO_3 and HCO_3 were determined by titration (EPA method 310.1, United States Environmental Protection Agency 1983); Cl, SO_4, and NO_3 were determined by ion chromatography. Concentrations are reported in meq l^{-1} to facilitate comparison of our solutions to solutions in other studies and because meq l^{-1} can be related easily to electrical conductivity, which is commonly reported in the context of salinity studies.

On 29 September 1993 (day 112) we measured the shoot length of every living seedling. We harvested all live seedlings in early October. To harvest, we lifted a planter and laid it horizontally in a water-filled basin. The planter was then slowly lifted upside down, leaving the substrate column and seedlings in the basin. We gently separated seedlings from the sand and water and measured total length of every harvested seedling. Mean root lengths were determined by subtracting the mean shoot length for a planter from the mean total length in that planter. Roots and shoots were separated for both species, and *P. fremontii* leaves were stripped from the stems. Roots, shoots, and leaves were dried at 60°C for 72 h and weighed.

One-way analysis of variance (SAS Institute, Inc. 1990) was used to assess the significance of treatment differences within the two species for five variables: percent of planted seeds alive at the end of the experiment ("end-of-season survival"), shoot length, root length, per-plant aboveground biomass, and per-plant root biomass. For all variables the mean value of the three planters in a tank was the unit of analysis. The arcsine transformation was applied to end-of-season survival values to meet the equal variance assumption (Snedecor and Cochran 1980).

Data from the Colorado Climate Center were used to determine the difference between precipitation and open-pan evaporation (adjusted with pan coefficient = 0.73) for the period 1 June–30 September 1993 in Fort Collins. Evaporation at Fort Collins exceeded precipitation by 26.2 cm during this period. The same calculation was made for the Bosque del Apache using data from the Western Regional Climate Center for the years 1975 through 1990. Precipitation data are from the Bosque del Apache National Wildlife Refuge, and open-pan evaporation data are from Socorro, NM (latitude 34°5′ north, longitude 106°53′ west, elevation 1399 m; pan coefficient = 0.73). Growing-season evaporation at the Bosque del Apache exceeded precipitation by an average of 40.6 cm; $n = 16$, maximum = 51.0 cm, and minimum = 32.3 cm during these 16 years.

We performed laboratory germination experiments in January 1994. Five 25-seed replicates of five salinity treatments were completely randomized for both *T. ramosissima* and *P. fremontii*. Seeds were sowed in 7.5-cm petri dishes containing a Whatman #3 filter and 7 ml of a treatment solution. Petri dishes were placed in a Percival Model I-35 biological incubator after sealing the dish tops with Parafilm. Temperature in the incubator was 20°C throughout the experiment, and petri dishes were exposed to 16 h of light and 8 h of darkness each day. Four of the treatment solutions

were the same as those used in the establish-ment experiment (0, 1, 3, and 5 times the concentration of the Rio Grande at San Marcial, NM); the fifth solution contained 7 times the concentration of the Rio Grande. Germinants in every petri dish were counted after seven days. A seed was considered germinated if it exhibited expanded cotyledons and an elongated radicle. The arcsine transformation was applied to percent germination values to meet the equal variance assumption, and one-way analysis of variance was performed on the transformed values (SAS Institute, Inc. 1990). When germination equaled 100%, the proportion was counted as $(n - 0.25)/n$, where n = the number of seeds planted (Snedecor and Cochran 1980).

RESULTS

EC and pH in the tanks varied little within treatments over the course of the experiment (Table 1). Mean temperature in the tanks was 21.7°C (standard error = 0.8, $n = 17$). Concentrations of measured chemical constituents in different treatments did not increase proportionally to the quantities of salt originally added, indicating that salts (especially $CaCO_3$) precipitated at higher concentrations (Table 1). Nevertheless, concentrations increased across treatments, with total concentrations ranging from 0.7 meq l^{-1} (0.11 dS m^{-1}) in treatment 0x to 37.4 meq l^{-1} (3.45 dS m^{-1}) in treatment 5x (Table 1).

For *P. fremontii* there was a significant treatment effect ($P = .003$) on end-of-season survival, but not on any of the four measured growth variables (Table 2). End-of-season survival was negatively associated with increasing salinity: survival was greatest in treatment 0x and lowest in treatment 5x. Because the end-of-season survival variable combines germination and mortality, we analyzed the arcsine-transformed number of seedlings 7 d after planting (germination), and the arcsine-transformed difference between germination and end-of-

TABLE 1. Chemical analysis of tank water for four treatments in the outdoor establishment experiment in Fort Collins, CO. For ion concentrations ($n = 4$), minimum and maximum values are presented in parentheses below treatment means. For electrical conductivity ($n = 51$) and pH ($n = 42$), means ± 1 standard error are presented.

Factor	Treatment			
	0x	1x	3x	5x
Ca (mmol l^{-1})	0.36 (0.20, 0.52)	1.82 (1.71, 2.00)	4.02 (3.49, 4.83)	4.54 (3.02, 7.02)
Mg (mmol l^{-1})	0.11 (0.08, 0.16)	0.60 (0.46, 0.75)	1.65 (1.47, 1.97)	2.62 (2.28, 2.97)
Na (mmol l^{-1})	0.17 (0.09, 0.28)	4.85 (4.41, 5.11)	13.87 (11.91, 15.49)	22.24 (19.33, 24.65)
K (mmol l^{-1})	0.08 (0.06, 0.09)	0.26 (0.20, 0.34)	0.51 (0.44, 0.55)	0.79 (0.72, 0.90)
HCO$_3$ (mmol l^{-1})	1.04 (0.62, 1.44)	3.92 (3.24, 4.44)	8.34 (7.29, 9.96)	9.60 (5.87, 15.74)
Cl (mmol l^{-1})	0.10 (0.07, 0.14)	2.47 (1.88, 2.82)	7.10 (6.96, 7.31)	12.12 (10.88, 13.21)
SO$_4$ (mmol l^{-1})	0.04 (0.04, 0.05)	1.66 (1.32, 1.86)	5.06 (4.76, 5.32)	7.73 (7.13, 8.33)
NO$_3$ (mmol l^{-1})	0.03 (0.002, 0.08)	0.03 (0.006, 0.09)	0.05 (0.01, 0.08)	0.06 (0.02, 0.15)
Total cations (meq l^{-1})	1.2 (0.7, 1.6)	10.0 (9.2, 10.8)	25.7 (23.8, 26.7)	37.4 (34.5, 41.5)
EC (dS m^{-1})	1.09 ± 0.03	0.97 ± 0.11	2.37 ± 0.23	3.45 ± 0.39
pH	7.54 ± 0.03	8.10 ± 0.02	8.29 ± 0.02	8.05 ± 0.03

TABLE 2. Survival and growth of *Populus fremontii* and *Tamarix ramosissima* seedlings exposed to four different salinity treatments for one growing season outdoors in Fort Collins, CO. High and low replicate means are given in parentheses below the treatment means ($n = 3$). Treatment effects were analyzed by completely randomized one-way ANOVA. Survival ANOVA was performed on arcsine-transformed data.

Species Variable	Treatment				F	P
	0x	1x	3x	5x		
Cottonwood						
Survival (% of planted seed)	57.0 (50.0, 63.0)	49.3 (45.7, 54.0)	46.6 (41.0, 51.0)	29.0 (20.7, 35.0)	11.4	.003
Shoot height (mm)	33.9 (32.8, 34.5)	36.3 (34.5, 38.5)	39.6 (36.5, 43.9)	38.3 (34.7, 40.8)	2.6	.13
Root length (mm)	239.2 (227.1, 258.4)	280.9 (257.8, 309.3)	286.9 (253.6, 311.7)	247.4 (206.3, 274.6)	2.1	.17
Per-plant shoot biomass (mg)	14.1 (13.7, 14.4)	14.6 (11.2, 16.6)	21.4 (18.9, 25.8)	19.8 (14.3, 25.9)	2.8	.11
Per-plant root biomass (mg)	26.8 (21.2, 35.5)	19.6 (16.4, 21.3)	31.8 (21.6, 43.2)	31.2 (17.2, 42.9)	1.1	.41
Saltcedar						
Survival (% of planted seed)	42.3 (29.5, 51.6)	37.8 (33.8, 42.0)	37.3 (31.8, 40.8)	29.5 (22.8, 35.2)	1.6	.26
Shoot height (mm)	18.1 (17.3, 18.8)	17.7 (15.5, 19.8)	18.2 (15.6, 22.2)	18.3 (18.2, 18.3)	0.04	.99
Root length (mm)	174.4 (166.4, 184.9)	173.6 (154.8, 192.9)	179.0 (128.1, 243.6)	162.0 (147.2, 169.5)	0.15	.92
Per-plant shoot biomass (mg)	5.5 (4.8, 6.2)	5.5 (4.1, 6.4)	6.3 (4.3, 9.6)	6.2 (5.8, 6.4)	0.22	.88
Per-plant root biomass (mg)	7.7 (7.1, 8.9)	7.3 (5.5, 9.2)	9.9 (7.0, 14.7)	9.5 (7.6, 12.1)	0.74	.56

season survival (mortality). There was a significant treatment effect on germination ($P = .008$), but not on mortality ($P = .45$), indicating that the effect on end-of-season survival was predominantly due to lower germination at higher salt concentrations. For *T. ramosissima* there were no significant treatment effects (Table 2).

Although *P. fremontii* germination in outdoor tanks was significantly decreased at high salinity, laboratory germination was not similarly affected even at seven times the salinity of the Rio Grande, total concentration 48.4 meq l^{-1} (4.56 dS m^{-1}; Table 3). There was a significant positive effect of increasing salinity on *T. ramosissima* germination ($P = .03$) (Table 3).

DISCUSSION

The absence of a negative effect of salinity on *P. fremontii* germination in the laboratory at concentrations as high as 48.4 meq l^{-1} (4.56 dS m^{-1}) is consistent with results of earlier studies. Jackson et al. (1990) found that *P. fremontii* germinated in the laboratory at salinities of 0, 27, and 106 meq l^{-1} using a mixture of NaCl and $CaCl_2$, but not at 319 meq l^{-1} or above. Siegel and Brock (1990) observed higher percent germination of *P. fremontii* in the laboratory in NaCl solutions of 0, 25, and 50 meq l^{-1} than at 100 meq l^{-1} and above. Therefore, *P. fremontii* is no more sensitive to the mix of salts present in the Rio Grande than to NaCl and $CaCl_2$ solutions of equal strength. Tests at higher salinities with the same ionic ratios were not possible with our Rio Grande mix because of low solubilities of some of the constituent salts. The decrease in *T. ramosissima* germination at low salinity in the laboratory (Table 3) is consistent with the finding by Jackson et al. (1990) that germination increases between 0 and 106 meq l^{-1}.

Our results indicate that a given water salinity may negatively affect germination of *P.*

TABLE 3. Percent germination of *Populus fremontii* and *Tamarix ramosissima* seedlings exposed to five salinity treatments in covered petri dishes. High and low replicate values are given below the treatment mean ($n = 5$). Treatment effects were analyzed by completely randomized one-way ANOVA using arcsine-transformed data.

Species	Treatment					F	P
	0x	1x	3x	5x	7x		
Cottonwood	90.4	96.0	96.0	92.8	96.0	1.2	.35
	(80.0, 100.0)	(92.0, 100.0)	(92.0, 100.0)	(84.0, 96.0)	(92.0, 100.0)		
Saltcedar	69.6	68.8	78.4	84.8	84.0	3.3	.03
	(60.0, 88.0)	(56.0, 80.0)	(68.0, 92.0)	(76.0, 92.0)	(76.0, 92.0)		

fremontii seeds under ambient conditions but not under laboratory conditions. This may have resulted from an interaction between the effects of salinity and soil moisture content, or from vapor-pressure deficit differences. In outdoor planters, but not laboratory petri dishes, evaporation of water may have resulted in lower soil moisture and higher salt concentration at the soil surface. These factors would both tend to reduce soil water potential, thereby increasing plant water stress. Because the difference between evaporation and precipitation is somewhat greater at the Bosque del Apache than in Fort Collins, the effect of salinity might be stronger at the Bosque, especially in dry years. Finally, greater vapor-pressure deficits in the field relative to the laboratory may have exacerbated plant water stress.

Salinity appears to be a relatively minor factor regulating numbers of *P. fremontii* and *T. ramosissima* seedlings on freshly deposited sandbars along the Rio Grande. The only significant effects of increasing salinity were a small decrease in *P. fremontii* germination in outdoor planters and a small increase in *T. ramosissima* germination in the laboratory. There were no significant effects on survival after germination or above- or belowground growth for either species, even at water salinities several times that of the Rio Grande. The presence of abundant seedlings of *P. fremontii* and *T. ramosissima* on sandbars along the Rio Grande in most years is consistent with our results.

Although salinity may play only a minor role in the colonization of newly deposited alluvial bars by *T. ramosissima* and *P. fremontii*, this factor can become more important over time. Over many years salt becomes concentrated on some floodplains as a result of evaporation and salt extrusion from *T. ramosissima* leaves. EC readings as high as 10.0 dS m^{-1} have been reported in floodplain sediment at the Bosque

del Apache (John Taylor, Bosque del Apache National Wildlife Refuge, personal communication), and soil salinity levels as high as 60,000 mg l^{-1} occur on floodplain sites along the lower Colorado River (Jackson et al. 1990). Soil EC above 2.0 dS m^{-1} can reduce the growth of *P. fremontii* pole plantings (Anderson 1989). *T. ramosissima* has been shown to be less susceptible than *P. fremontii* to many of the negative effects of higher salinities (Brotherson and Winkle 1986, Jackson et al. 1990). *Tamarix* species avoid harmful effects of salts through extrusion from leaves and cellular compartmentation (Berry 1970, Kleinkopf and Wallace 1974, Waisel 1991).

Our results could be applied to efforts to revegetate riparian areas from seed. Riparian revegetation in the Southwest has largely consisted of planting poles or potted shoot cuttings. Although these approaches have been successful in some areas (Anderson et al. 1990), they can cost up to $10,000 per hectare (Ohmart et al. 1988). Furthermore, they require the destruction of parts of existing trees, and often entire trees or stands. Finally, these approaches may require importing cuttings or poles adapted to different site conditions. One alternative is regeneration of native cottonwoods and willows using natural seedfall (Friedman 1993, John Taylor personal communication). This approach generally involves clearing and irrigating an area so that seeds from nearby trees can colonize it. Our results suggest that water as saline as 37.4 meq l^{-1} (EC 3.45 dS m^{-1}) can be used to grow *P. fremontii* from seed on sand (Tables 1, 2). However, care must be taken to prevent long-term salt accumulation through evaporation (e.g., through periodic flooding to flush salts) and to avoid sites with preexisting high salinity. Use of water with low salinity can help prevent negative effects on *P. fremontii* and may decrease the

germination rate of *T. ramosissima* (Table 3). However, in a restoration effort along the Cache la Poudre River, *T. ramosissima* became established in large numbers along with *P. deltoides* in spite of use of water of low salinity (Douglas Gladwin, National Biological Survey, personal communication). Therefore, low salinity will not prevent establishment of *T. ramosissima* from seed when moisture, a bare sediment, and a seed source are present.

ACKNOWLEDGMENTS

LITERATURE CITED

ANDERSON, B. W. 1989. Research as an integral part of revegetation projects. Pages 413–419 *in* D. L. Abell, technical coordinator, Proceedings of the California Riparian Systems Conference: protection, management, and restoration for the 1990s. USDA Forest Service General Technical Report PSW-110. Berkeley, CA.

ANDERSON, B. W., A. HIGGINS, AND R. D. OHMART. 1977. Avian use of saltcedar communities in the lower Colorado River Valley. Pages 128–136 *in* R. R. Johnson and D. A. Jones, technical coordinators, Importance, Preservation, and Management of Riparian Habitat: a symposium. USDA Forest Service General Technical Report RM-43. Fort Collins, CO.

ANDERSON, B. W., E. R. MILLER, AND J. P. WASHINGTON. 1990. Revegetation on the Kern River preserve 1986–1989. Research report prepared for The Nature Conservancy and California Department of Fish and Game. Revegetation and Wildlife Management Center, Inc., Blythe, CA. 19 pp.

BERRY, W. L. 1970. Characteristics of salts secreted by *Tamarix aphylla*. American Journal of Botany 57: 1226–1230.

BLACKBURN, W. H., R. W. KNIGHT, AND J. L. SCHUSTER. 1982. Saltcedar influence on sedimentation in the Brazos River. Journal of Soil and Water Conservation, 37: 298–301.

BOWSER, C. W. 1958. Introduction and spread of the undesirable tamarisks in the Pacific southwestern section of the United States and comments concerning the plants' influence upon the indigenous vegetation. Pages 12–16 *in* Symposium on Phreatophytes. American Geophysical Union, Sacramento, CA.

BROTHERSON, J. D., AND V. WINKEL. 1986. Habitat relationships of saltcedar (*Tamarix ramosissima*) in central Utah. Great Basin Naturalist 46: 535–541.

BUSCH, D. E., AND S. D. SMITH. 1993. Effects of fire on water and salinity relations of riparian woody taxa. Oecologia 94: 186–194.

_____. In press. Decline, persistence, and competition of woody taxa in riparian ecosystems of the southwestern U.S. Submitted to Ecological Monographs.

CAMPBELL, C. J., AND W. A. DICK-PEDDIE. 1964. Comparison of phreatophyte communities on the Rio Grande in New Mexico. Ecology 45: 492–502.

COHAN, D. R., B. W. ANDERSON, AND R. D. OHMART. 1978. Avian population responses to salt cedar along the lower Colorado River. Pages 371–382 *in* R. R. Johnson and J. F. McCormick, technical coordinators, Strategies for Protection and Management of Floodplain Wetlands and Other Riparian Ecosystems: proceedings of the symposium. USDA Forest Service General Technical Report WO-12. Washington, DC.

EVERITT, B. L. 1980. Ecology of saltcedar—a plea for research. Environmental Geology 3: 77–84.

FRIEDMAN, J. M. 1993. Vegetation establishment and channel narrowing along a Great-plains stream following a catastrophic flood. Unpublished doctoral dissertation, University of Colorado, Boulder.

GRAF, W. L. 1978. Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. Geological Society of America Bulletin 89: 1491–1501.

GREENWAY, H., AND R. MUNNS. 1980. Mechanisms of salt tolerance in nonhalophytes. Annual Review of Plant Physiology 31: 149–190.

HARRIS, D. R. 1966. Recent plant invasions in the arid and semi-arid southwest of the United States. Annals of the Association of American Geographers 56: 408–422.

HORTON, J. S. 1977. The development and perpetuation of the permanent tamarisk type in the phreatophyte zone of the Southwest. Pages 124–127 *in* R. R. Johnson and D. A. Jones, technical coordinators, Importance, Preservation, and Management of Riparian Habitat: a symposium. USDA Forest Service General Technical Report RM-43. Fort Collins, CO.

HORTON, J. S., AND C. J. CAMPBELL. 1974. Management of phreatophyte and riparian vegetation for maximum multiple use values. USDA Forest Service Research Paper RM-117. 23 pp.

JACKSON, J., J. T. BALL, AND M. R. ROSE. 1990. Assessment of the salinity tolerance of eight Sonoran desert riparian trees and shrubs. Final report, U.S. Bureau of Reclamation Contract No. 9-CP-30-07170. Biological Sciences Center, Desert Research Institute, University of Nevada System, Reno. 102 pp.

KLEINKOPF, G. E., AND A. WALLACE. 1974. Physiological basis for salt tolerance in *Tamarix ramosissima*. Plant Science Letters 3: 157–163.

MERKEL, D. L., AND H. H. HOPKINS. 1957. Life history of salt cedar (*Tamarix gallica* L.). Transactions of the Kansas Academy of Science 60: 360–369.

OHMART, R. D., B. W. ANDERSON, AND W. C. HUNTER. 1988. The ecology of the lower Colorado River from Davis Dam to the Mexico–United States International Boundary: a community profile. U.S. Fish and Wildlife Service Biological Report 85(7.19). 296 pp.

OHMART, R. D., W. O. DEASON, AND C. BURKE. 1977. A riparian case history: the Colorado River. Pages 35–47 *in* R. R. Johnson and D. A. Jones, technical coordinators, Importance, Preservation, and Management of Riparian Habitat: a symposium. USDA Forest Service General Technical Report RM-43. Fort Collins, CO.

ROBINSON, T. W. 1965. Introduction, spread and areal extent of saltcedar (*Tamarix*) in the western states. United States Geological Survey Professional Paper 491-A. 13 pp.

SAS INSTITUTE, INC. 1990. SAS/STAT user's guide, version 6, 4th edition. SAS Institute, Inc., Cary, NC.

SEGELQUIST, C. A., M. L. SCOTT, AND G. T. AUBLE. 1993. Establishment of *Populus deltoides* under simulated alluvial groundwater declines. American Midland Naturalist 130: 274–285.

SIEGEL, R. S., AND J. H. BROCK. 1990. Germination requirements of key Southwestern woody riparian species. Desert Plants 10: 3–8, 34.

SNEDECOR, G. W., AND W. G. COCHRAN. 1980. Statistical methods. Iowa State University Press, Ames. 507 pp.

STROMBERG, J. C., D. T. PATTEN, AND B. D. RICHTER. 1991. Flood flows and dynamics of Sonoran riparian forests. Rivers. 2: 221–235.

TOMANEK, G. W., AND R. L. ZIEGLER. 1962. Ecological studies of salt cedar. Unpublished report, Division of Biological Sciences, Fort Hays Kansas State College, Hays. 128 pp.

UNITED STATES ENVIRONMENTAL PROTECTION AGENCY. 1983. Methods for chemical analysis of water and wastes. Publication identification: EPA-600 4-79-020. Environmental Monitoring and Support Laboratory, Office of Research and Development, Cincinnati, OH.

UNITED STATES GEOLOGICAL SURVEY. 1991. Water resources data. New Mexico, water-year 1990. U.S. Geological Survey water-data report NM-90.

_____. 1992. Water resources data. New Mexico, water-year 1991. U.S. Geological Survey water-data report NM-91.

WAISEL, Y. 1991. The glands of *Tamarix aphylla*: a system for salt secretion or for carbon concentration? Physiologia Plantarum 83: 506–510.

WARREN, D. K., AND R. M. TURNER. 1975. Saltcedar (*Tamarix chinensis*) seed production, seedling establishment, and response to inundation. Journal of the Arizona Academy of Science 10: 135–144.

ZASADA, J. C., AND R. DENSMORE. 1977. Changes in Salicaceae seed viability during storage. Seed Science and Technology 5: 509–517.